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ORIGINAL PAPER

The effect of windthrow and its management on breeding bird communities in a managed forest

Michał Żmihorski

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Abstract This study aimed to evaluate the impact of windthrow and two types of its management on the bird community of a managed, pine-dominated forest (NE Poland), where a windstorm event occurred in 2002. In 2007, the bird species composition was assessed using the point count method in three types of habitat: windthrow left undisturbed for natural regeneration, managed windthrow (all fallen trees removed), and intact forest (undisturbed by the windstorm, used as the control). In total, 2,365 individual birds of 70 species were recorded in the three analyzed habitats. The mean number of individuals per point and species per point was significantly higher in the natural windthrow than in the two other habitats. The diversity of the bird community was higher in the natural and managed windthrow, as compared to the control. The bird community of the control was significantly more similar to that of the natural windthrow than to the one in the managed windthrow. These results lead to a conclusion that the bird community was affected more by the clearing and artificial replanting following the windthrow than by the windthrow itself.

Keywords Clearcuts · Dead wood · Disturbances · Salvage logging · Species diversity · Timber · Windstorm

Introduction

In forest ecosystems of Central and Northern Europe as well as in North America, disturbances play an important role in shaping the spatial structure of a phytocoenosis and composition of forest dwelling animal communities. Fires, windstorms or outbreaks of folivorous insects created open areas in primeval forests and are today thought to be an important environmental factor in many forest ecosystems (Schmiegelow et al. 1997; Svenning 2002; Lindbladh et al. 2004). However, in managed forests, these disturbances are usually regarded as undesirable, since they can significantly reduce the quality and

M. Żmihorski (✉)
Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warsaw, Poland
e-mail: zmihorski@miiz.waw.pl

quantity of timber (Schelhaas et al. 2003). Therefore, in modern forestry, the impact of disturbance agents is largely suppressed in comparison to primeval conditions (Kuuluvainen 2002; Schelhaas et al. 2003). On the other hand, forest ecosystems are currently believed to be much more dynamic, variable and unstable than was previously thought. As a result, attitudes towards the significance of disturbances have changed considerably in the last 20 years (Wu and Loucks 1995). It seems that they are important in biodiversity conservation, because areas affected by disturbances create habitats for many early-successional species that do not occur in mature stands, leading to an increase in species richness (Niemelä 1999; Bengtsson et al. 2000; Ulanova 2000; Drever et al. 2006). Since biodiversity preservation is one of the goals of modern forest management, knowledge concerning disturbances is crucial and has recently attracted the attention of forest managers. In light of the significance of disturbances for a forest ecosystem's biodiversity, the suppression of disturbances and management practices of disturbed areas applied to date in managed forests are most probably inappropriate. An important question arises: to what extent should the effects of disturbances be removed in order to achieve the optimal maintenance of forest biodiversity and timber production in managed forests?

After a windstorm or fire event, the intervention of foresters may be necessary to regain at least part of the timber and reduce the possibility for other calamities related to windthrow or fire-affected areas to spread (e.g. windthrow can be followed by pest outbreaks, Bouget and Duelli 2004; Eriksson et al. 2007). On the other hand, some facts indicate that human intervention in mitigating disturbance effects should be restricted. First, disturbed patches (e.g. windthrow) are gradually settled by many plant and animal species of conservation concern (e.g. Reier et al. 2005). For this reason, they can be treated as biodiversity hotspots (Fuller 2000; Bouget and Duelli 2004). Second, removal of damaged trees and re-growth of disturbed patches may not be economically justified. Most commonly, timber quality is seriously reduced by the disturbance agent and natural tree stand regeneration can substitute for more expensive artificial replanting. It is also important to mention that disturbed habitats are of great scientific value. Research conducted in disturbed patches has considerably improved our understanding of natural processes that operate in forest ecosystems, which is crucial for developing optimal forest management methods (Niemelä 1999). Therefore, forest management improvement practices in disturbed areas urgently require further research, especially as climate changes may affect the intensity and frequency of disturbances in the future (Peltola et al. 1999; Schelhaas et al. 2003).

The aim of this study was to assess changes in the bird community related to a natural disturbance (i.e. large windthrow) and the impact of further management of the windthrow on this community. The most important question that I posed was: what is the extent of forest bird community transformation caused by clearing and replanting a windthrow, relative to a windthrow left to regenerate naturally?

Materials and methods

Study area

The study was conducted in North-Eastern Poland, in the Piska Forest, which is a ca. 90,000 ha forest complex. Its tree stand is managed by the National Forest Holding for timber production and is composed mainly of pine (*Pinus sylvestris*), with a lesser proportion of spruce (*Picea abies*) and oak (*Quercus robur*). In general, the forest is comprised

of poor habitats located in a young glacial landscape, with sandy soils and the forest floor's vegetative understory dominated by mosses (*Polytrichum* spp.), grasses (*Deshampsia flexuosa*) and shrubs (*Vaccinium* spp.). The age structure of the stand was highly diversified and ranged from 0 years in fresh clearcuts to 100–150 years in the oldest patches. Clearcutting is used as the main harvesting technique and new stands regrow as the result of man-made afforestation using locally indigenous species for planting.

On July 4, 2002, a windstorm damaged ca. 15,000 ha in the Piska Forest and created one of the largest windthrows ever recorded in Poland. The forest was changed into a mosaic of open areas (completely damaged stands covered ca. 40% of the windthrow area), partially destroyed stands with single trees, groups of trees or small areas covered by undisturbed forest (ca. 10% of the forest affected by the windstorm). In the following years, most of the damaged stands were cleared and replanted, according to official forest management rules. However, a small area (445 ha) was excluded from the foresters' activities and left to regenerate naturally.

Bird counts were performed in three different habitats situated in the Piska Forest. The habitats were: (1) windthrow left for natural regeneration, (2) managed (i.e. cleared) windthrow and (3) undisturbed managed forest (Fig. 1). The windthrow left to regenerate naturally (hereafter "natural windthrow") covered a 445 ha windthrow area, which had

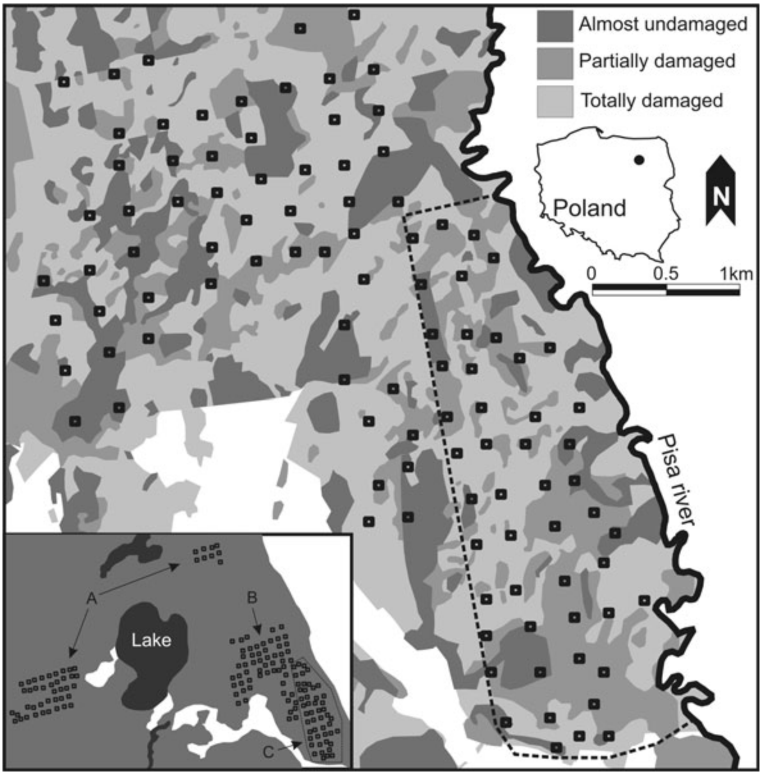

Fig. 1 *Smaller frame*: distribution of all 155 count points (*squares*) in Piska Forest (NE Poland) in the control habitat (*A*), managed windthrow (*B*) and natural windthrow (*C*, bordered with *broken line*). *Larger frame*: detailed distribution of count points (*squares*) placed in natural windthrow (bordered with *broken line*) and in managed windthrow (remaining *squares*)

been excluded from clearing and artificial regeneration. This site abounded in fallen logs, leaning trees and broken trunks, among which were numerous seedlings of pines, birches and oaks. There were also some partially or completely undisturbed forest patches (up to several ha). The cleared windthrow (hereafter "managed windthrow") habitat covered an extensive part of the damaged forest, where all the fallen, leaning and broken trees were removed. Artificial replanting, partially fenced to protect against ungulates, had been applied there. Small patches of undisturbed forest could also be found, in size and number similar to that in the natural windthrow. The undisturbed managed forest (hereafter "control") was a typical managed stand representative of the entire Piska Forest before the windstorm event. The natural and managed windthrow habitats were adjacent to each other, but the control was approximately 5 km west of these two sites. This allowed me to exclude the impact of the windstorm on the bird community in the control habitat.

Bird sampling

A series of bird counts were conducted in the spring of 2007, almost 5 years after the windstorm event. 155 census points were selected in the three habitats (ca. 50 points/habitat). Census points were located at the intersections of a 300 m × 300 m grid superimposed on the study area (the points were situated 300 m from one another, see also Ralph et al. 1995 who recommend 250 m between point counts as a minimum distance). Birds were counted using a fixed-radius point count (Gregory et al. 2004), which is one of the most common methods used for bird monitoring and ecological research (see Fuller 2000; Dunford and Freemark 2005; Paquet et al. 2006; Gregory et al. 2007; Venier and Pearce 2007; Greenberg et al. 2008; Uezu et al. 2008). There were 49 count points in the natural windthrow, 57 in the managed windthrow and 49 in the control. The exact location of each point was marked by using GPS. Two 10-min counts were conducted at each point, one in April and one in June. This method allowed the detection of both early sedentary breeders and tropical migrants, which start to breed later in the spring. The points were sampled in random order. During the 10-min counts, I recorded all individuals heard or seen up to a 100 m circumference (which is the radius often used in bird monitoring schemes—Dunford and Freemark 2005; Giraudo et al. 2008). In order to exclude migrants, birds in flight were not recorded. All counts were performed in the morning (before 10 a.m. in April and before 9 a.m. in June) and only in good weather conditions (no strong wind or rainfall). Of the two censuses carried out at a given point, the maximum number of each species was used for further analysis (e.g. Hausner et al. 2003; Barbaro et al. 2007).

Statistical analysis

Since the count points were located close to one another, a simplified measure of spatial autocorrelation was used to check whether the sampling points could be treated as independent measures. I correlated the spatial distance and the improved Jaccard similarity index (see below) for 50 randomly chosen point pairs in each habitat type. The similarity of the bird communities between two compared count points was only barely explained by the distance between the points. Distance explained only 0.3–8.5% of the variation of the improved Jaccard similarity index computed for the point pairs. The correlation between distance and similarity was significant for the natural windthrow ($P = 0.04$) and not significant for the managed windthrow and control ($P = 0.082$ and $P = 0.711$ respectively).

Redundancy analysis (RDA) was used to show species-habitat type correlations. The location of each sampling point (natural windthrow, managed windthrow and control) was

used as a habitat variable in CANOCO software. The Monte-Carlo test with 500 permutations was used to test the significance of the canonical axes (Lepš and Šmilauer 2003). The average number of individuals and the average species number obtained per point were compared between the three habitats by means of the one-way ANOVA (or the Kruskal–Wallis nonparametric ANOVA) and the LSD post-hoc test (or the Mann–Whitney test, in the case of variance non-homogeneity). The rarefaction method was applied to compare bird community diversity using EstimateS 8.0.0. (Colwell 2005). The diversity of the bird community in each habitat type was presented as the expected cumulative number of bird species for 716 randomly chosen bird individuals (on the basis of 1,000 randomization runs of sample selection, separately for each habitat type). This value was used because the smallest number of individuals sampled in one habitat was 716. Similarities of the bird communities recorded in the three habitat types were also assessed. The mean similarity index was computed for two randomly chosen points from two compared habitats (natural windthrow vs. managed windthrow, natural windthrow vs. control, managed windthrow vs. control). In order to obtain the average similarity index for these comparisons, I computed the similarity index for 11,935 pairs of points (i.e. all possible combinations of point pairs). The improved Jaccard similarity index was used for this purpose, which covers species abundance (the classical Jaccard index is based only on occurrences) and corrected for unseen species in the compared samples (hereafter improved Jaccard index; Chao et al. 2005). As was shown, the improved Jaccard index is much more reliable than the classical index (Chao et al. 2005). The similarity computations were performed with the shared species function in EstimateS 8.0.0. (Colwell 2005). SPSS 13.0 was used for all statistical analyses.

Results

In the three analyzed habitats, 2,365 bird individuals belonging to 70 species were recorded (Fig. 2). The Chaffinch (*Fringilla coelebs*) was the most abundant species in the three habitat types, but some species associated with open areas also played an important role in the community (e.g. Wood Lark *Lullula arborea*, Yellowhammer *Emberiza citrinella*, Tree Pipit *Anthus trivialis*). The abundance of many bird species varied greatly between the habitats. Several species, including some forest specialists, were most abundant in the natural windthrow (e.g. Great Spotted Woodpecker *Dendrocopos major*, Winter Wren *Troglodytes troglodytes* or Song Thrush *Turdus philomelos*), whereas birds associated with the managed windthrow were predominantly open habitat specialists or edge-dwelling species, such as Skylark *Alauda arvensis*, Yellowhammer, Woodlark, Northern Wheatear *Oenanthe oenanthe* or White Wagtail *Motacilla alba* (Fig. 2). Chaffinch, Wood Warbler *Phylloscopus sibilatrix*, Coal Tit *Periparus ater* and Crested Tit *Lophophanes cristatus* and other forest specialists were recorded predominantly in the intact stand (i.e. control habitat). The bird communities differed significantly among the three habitats (Monte-Carlo test of significance of first canonical axis, F ratio $= 13.38$, $P = 0.002$; Monte-Carlo test of significance of all canonical axes, F ratio $= 9.77$, $P = 0.002$).

The density (all individuals/point) of the entire bird community also varied between habitats, denoted 17.4 for the natural windthrow, 14.0 for the managed windthrow and 14.6 for the control (Fig. 3). The mean density in the natural windthrow was higher than in the managed windthrow (post-hoc LSD, $P < 0.001$) and the control ($P < 0.001$). In contrast, there were no significant differences between the mean bird density in the managed windthrow and the control ($P = 0.42$). A similar pattern was obtained for the mean species

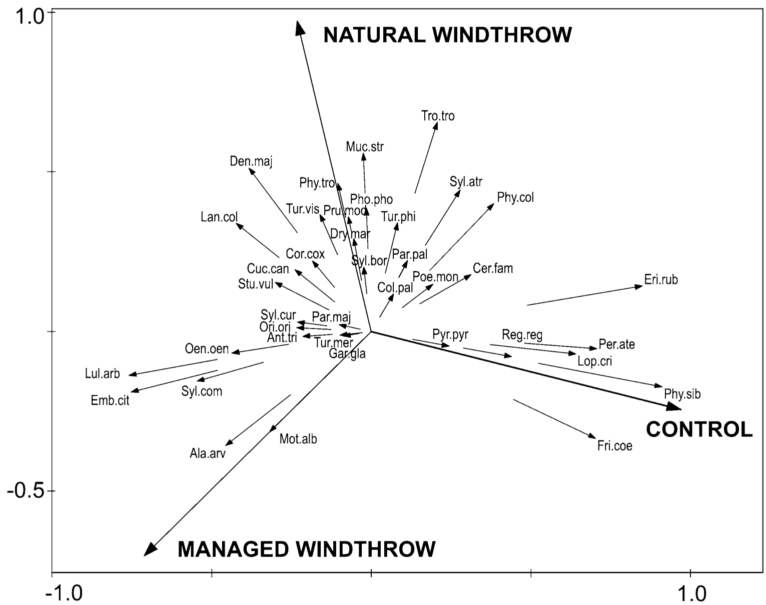

Fig. 2 Birds-habitat type biplot from the redundancy analysis (RDA) showing variability of the bird community in the three habitat types. Only species of abundance ≥ 5 individuals were included, abbreviations of species names include the first three letters of the genus and species scientific names

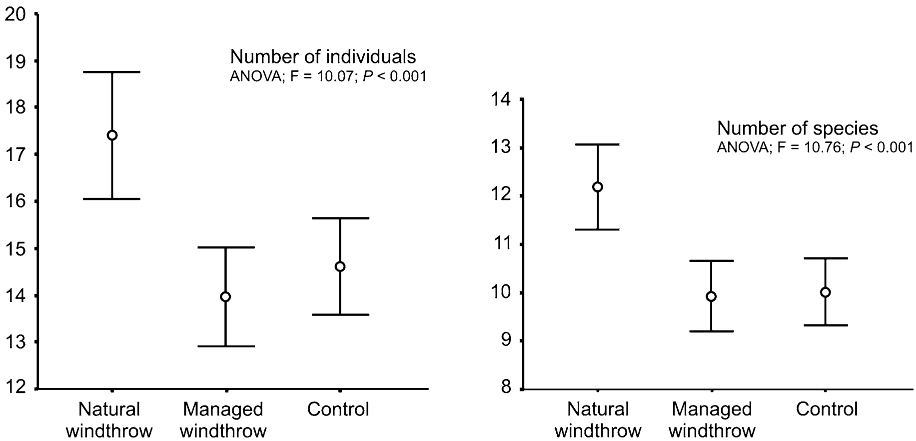

Fig. 3 Mean number of bird individuals and species recorded at a count point in three types of habitat in the Piska Forest; whiskers denote 95% confidence intervals. The variance homogeneity assumption was met in both cases (Levene test, $P > 0.213$ in both cases) and variables were normally distributed (Kolomogorov–Smirnov test, $P > 0.123$ in both cases)

number per count point. There were on average 12.2 species per point in the natural windthrow, 9.9 in the managed windthrow and 10.0 in the control (Fig. 3). The average species number per point in the natural windthrow was significantly higher compared to both the managed windthrow and the control (post-hoc LSD, $P < 0.001$ in both cases).

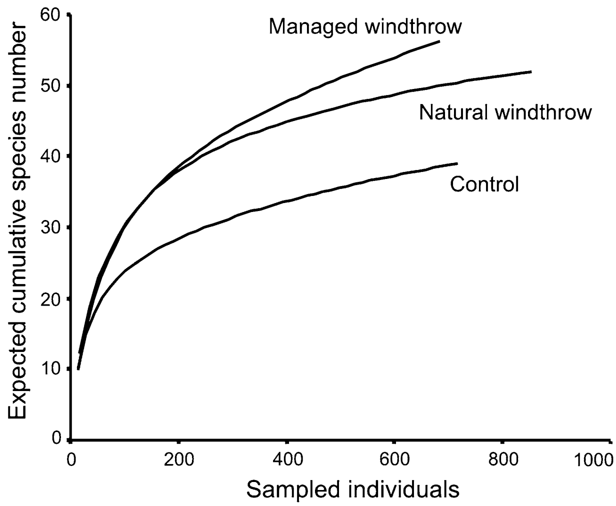

Fig. 4 The expected cumulative number of bird species as a function of the number of sampled bird individuals in three habitat types in the Piska Forest

However, there were no significant differences between the managed windthrow and the control ($P = 0.87$).

The species diversity of bird communities was lowest in the control and highest in the managed windthrow. For the 716 randomly chosen bird individuals, the expected cumulative number of bird species was 50.4 in the natural windthrow, 57.1 in the managed windthrow and 39.0 in the control (Fig. 4).

The average improved Jaccard similarity indices, computed for all possible between-habitat point-pairs, showed marked differences (Fig. 5). The lowest similarity was

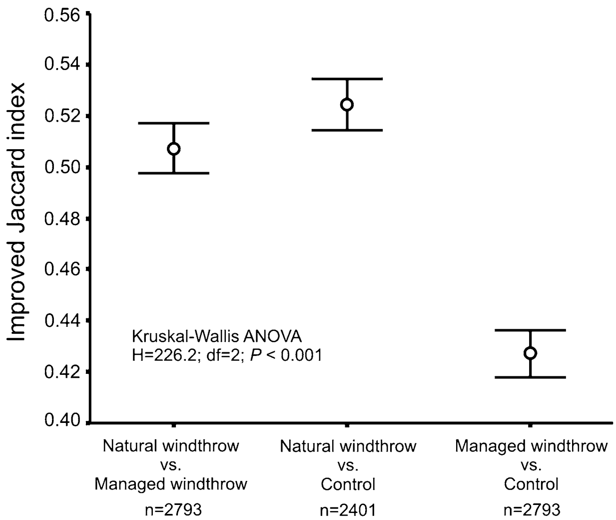

Fig. 5 The average value of the improved Jaccard similarity index, computed for all available point pairs (n) between habitat types; *whiskers* denote 95% confidence intervals

observed in the case of the bird communities in the control and managed windthrow habitats, and it significantly differed from the two other pairs of habitats (Mann–Whitney test, $P < 0.001$ in both cases). The control and the natural windthrow were the most similar, and the average values of the improved Jaccard similarity index obtained for this pair of habitats were higher than in the case of the control and the managed windthrow (Mann–Whitney, $P = 0.014$).

Discussion

This study concerned only one windthrow, albeit a large one, and so it is not possible to generalize with confidence. This is a common problem with studies of natural disturbances, which are often unpredictable in time and space. However, the size of this windthrow (ca. 15,000 ha) means that it affected a diverse array of environments within an extensively managed forest, increasing the likelihood that results will have broad application for similar events in managed forests elsewhere. Moreover, the low level (or lack) of spatial autocorrelation indicates that the adjacent point counts were independent and allow reliable inferences to be made.

The species composition recorded during the study is comprised of mainly common ones and no rare birds were recorded, such as raptors, woodpeckers or galliformes. Moreover, fewer species seem to be associated with the control area relative to the two remaining habitats. This most probably is due to the transformation of the forest structure related to management practices for producing timber (Wesołowski 2005). As a result of the disturbance, many non-forest species occurred. Interestingly, some of the birds that benefited from the windthrow (e.g. Woodlark, Northern Wheatear, Red-backed Shrike *Lanius collurio*, Yellowhammer) are open-country birds that have declined substantially in the farmland of parts of Europe (BirdLife International 2004). This leads to a suggestion that disturbed areas may provide a local refugium for some birds of conservation concern (see also Paquet et al. 2006). Therefore, evaluation of the disturbed stands as habitat for rare or declining species should not be disregarded, but further research is required on the effects of continued management (e.g. clearing, replanting) on the species.

Species diversity, expressed as the expected cumulative number of bird species for a given number of individuals sampled in the natural windthrow and managed windthrow habitats, increased relative to control. It can be concluded that the windthrow event led to an increase in bird species' diversity independently of the windthrow management mode. This was probably caused by the windstorm creating new habitats in the homogenous, closed-canopy forest, because many species that prefer open areas and forest clearings occurred in the disturbed habitats (Fig. 2 in this study, see also Fuller 2000; Faccio 2003; Paquet et al. 2006). A similar pattern was observed in the case of plant communities (Ulanova 2000; von Oheimb et al. 2007) and this may probably be a general rule, in accordance with the moderate disturbance hypothesis (e.g. Molino and Sabatier 2001).

The data collected from the natural windthrow suggest that natural disturbances are associated with higher bird density than in intact forests. This indicates that natural disturbances occurring in forest ecosystems significantly increase habitat capacity (e.g. number of different microhabitats) and its attractiveness to birds (Greenberg and Lanham 2001). This pattern is most probably driven by a decrease in habitat homogeneity and the complexity of its spatial structure. It should also be mentioned that the increase in bird density was not recorded in the managed windthrow and that the average densities of bird communities in the managed windthrow and control did not differ.

The similarity of bird communities between the natural windthrow and the control was higher than between the managed windthrow and the control. Due to the habitat structure of the natural windthrow, with numerous fallen and broken trunks, its bird community resembled that of a typical, intact and closed-canopy forest. In other words, the features of the natural windthrow habitat functioned as a buffer for many species typical of undisturbed, closed-canopy forest. In turn, habitat differences between the managed windthrow and the control were so pronounced that the bird communities in these two habitats show low similarity. These observations seem to have great importance for evaluating the two different ways of managing a disturbed area. The results indicate that bird communities are affected more profoundly by the salvage logging (dead wood removal) following a windstorm than by the natural windstorm itself (Fig. 6). This complies very well with the opinion of Foster and Orwig (2006), who concluded that the "consequence of natural disturbances in forested areas is that managers often initiate activities that may impose greater ecosystem impacts than the disturbances themselves". The strong effect of salvage logging on breeding bird communities seems to be a general pattern and has been recorded in several studies (Koivula and Schmiegelow 2006; Lain et al. 2008).

Utilizing forests for timber production changes ecosystems (Tomiałojć and Wesołowski 2004; Wesołowski 2005). One of the most important ecosystem transformations related to timber production is reducing the impact of natural disturbances such as insect outbreaks, fires and windstorms (see e.g. official forest management rules in Poland), which were of great importance for creating open areas in primeval forest (Svenning 2002). As a consequence, naturally disturbed plots are rare in modern day managed forests. However, timber production results in creating open areas in the forest—clearcuts—which may be settled by species of conservation concern (Paquet et al. 2006; Theuerkauf and Rouys 2006). The following question is important in evaluating the impact of forest management on forest biodiversity: can clearcuts substitute for natural disturbances in a managed forest? The importance of this question for biodiversity conservation in forests has already been stressed (Niemelä 1999; Buddle et al. 2006; Schieck and Song 2006; Tero and Kotiaho 2007; Rosenvald and Lõhmus 2008). However, the lack of naturally disturbed areas as references makes comparison of natural open areas with anthropogenic ones difficult (Niemelä 1999). Therefore, protection of naturally disturbed areas is crucial for the comparison, and constitutes another argument against salvage harvesting a windthrow.

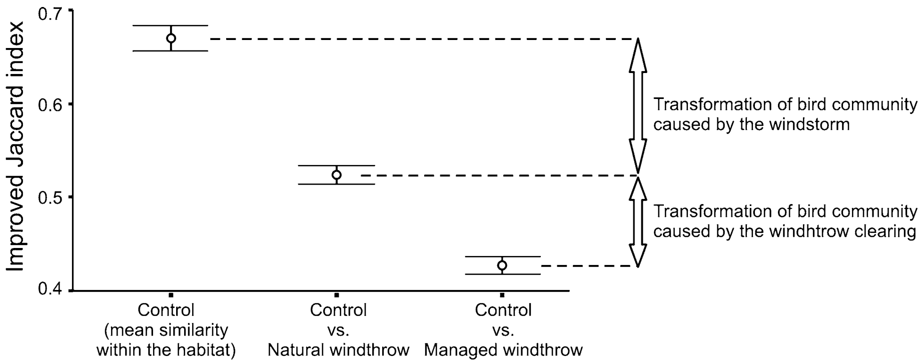

Fig. 6 Change in the bird community in two habitats created by windstorm (natural windthrow and managed windthrow) relative to control

The implication for management practices provided by this study is that allowing part of the fallen, broken or damaged trees in windthrow areas to remain is crucial for the persistence of forest dwelling birds in disturbed areas (this study, Schieck and Hobson 2000; Koivula and Schmiegelow 2006; see also Nitterus et al. 2007 for similar results in beetles community). This conclusion remains in agreement with most of the research conducted on this issue. Lindenmayer et al. (2004) provide several arguments against salvage logging and conclude that excluding large areas from salvaging is necessary. Also Foster and Orwig (2006) suggest that a conservative approach in the case of disturbed areas can be beneficial for the ecosystem. It should be emphasized that leaving some material in a managed forest seems to be economically justified. A case study of the Piska Forest showed that damage caused by the windstorm lowered the quality of timber, making its harvesting significantly less (up to ca. 40%) profitable (Kaliszewski A.—unpublished report on the economical justification of windthrow management). One may conclude that leaving some part of the dead wood in disturbed areas of managed forests is ecologically (and sometimes economically) justified.

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